NUTRIENT DENSITIES, CARBON: NITROGEN RATIOS, AND MIDDAY DIFFERENTIAL CANOPY TEMPERATURE IMPACT GRAIN YIELD OF STRESSED OAT

A. A. Jaradat[a]; W. E. Riedell[b]

[a] United States Department of Agriculture—Agricultural Research Service, Morris, Minnesota, USA [b] United States Department of Agriculture—Agricultural Research Service, Brookings, South Dakota, USA

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A. A. Jaradat[1] and W. E. Riedell[2]

[1]*United States Department of Agriculture—Agricultural Research Service, Morris, Minnesota, USA*

[2]*United States Department of Agriculture—Agricultural Research Service, Brookings, South Dakota, USA*

□ *Nutrient densities, carbon:nitrogen (C:N) ratio, and midday differential canopy temperature (dT), were assessed in oat plants subjected to biotic stresses during two years. Large portions of variation in nutrient densities and C:N ratio of leaves at the boot stage and of kernels and groats at harvest were negatively impacted by the 2- and 3-way interactions of leaves, kernels, and groats with the biotic stress treatments and years. The C:N ratios, but not nutrient densities, were always smaller in groats than in kernels, and during the stress than the no-stress year. Temporal variation accounted for a small variance associated with nutrients in leaves; whereas, stress treatments accounted for the largest variances associated with nutrients in kernels and groats. These indirect relationships among plant architecture components, dT, nutrient densities and C:N ratios, illustrate the complex interactions of biotic and abiotic stresses and their impact on grain yield and its components in oat.*

Keywords: C:N ratio, nutrient dynamics, biotic stress, yield models, oat

INTRODUCTION

Biotic and abiotic stresses disrupt the nutrient relationships in plants through their effects on nutrient availability, transport, and partitioning; however, biotic stresses, in particular, alter nutrient metabolism, especially nitrogen, and adversely affect grain quality traits which are relevant to human food and animal feed (Peterson et al., 2005). Whether caused by single or multiple factors, these stresses will suppress the development and proper

functioning of plant architectural components such as leaf initiation and expansion, tillering and leaf area index (LAI) (Kumar et al., 2006), and as a result of global climate change, are expected to increasingly impact crop yields (Kotchi, 2007). Canopy development, quantified by its architectural components, and its interaction with environmental and edaphic factors, determine the rate of transpiration and transpirational cooling, especially under stress conditions (Jackson et al., 1982). Canopy temperature under non-stress conditions was used as an indicator of potential yield performance under stress conditions (Rashid et al., 1999). However, midday differential canopy temperature (dT), which is based on the close, inverse relationship between canopy temperature and transpiration cooling (Jackson et al., 1982), is a better indicator of potential grain yield under stress than canopy temperature (Jaradat, 2007).

Photosynthate partitioning and yield potential under stress are, to some extent, determined by the carbon (C): nitrogen (N) ratio in plant organs (Borrás et al., 2004). Biotic stress reduces the nitrogen, but not the carbon, content of infected plant tissues; therefore, it increases the C:N ratio in stressed plants (Tartachnyk et al., 2006). This finding indirectly explains why plants infected by barley yellow dwarf virus partition a larger portion of biomass (i.e., fixed C) than uninfected plants to vegetative tissues (Persson et al., 2007).

Plants react to biotic stress first with changes in photosynthetic rate due to alteration of source-sink relationship and later with chlorophyll breakdown (Tartachnyk et al., 2006). Nutrients play a vital role in determining plant resistance, particularly to abiotic stress. The temporal multivariate relationships between nutrient densities in seeds and leaves and the unique cumulative variance for each nutrient are reliable indicators of whether a unique rate-limiting process is caused by stress (Grusak et al., 1999). In view of the complex interrelationships and interactions among the above-mentioned variables, understanding the factors that determine how efficiently crops can utilize environmental resources under different stresses may allow for better modeling of grain yield and its components as functions of dT, nutrient densities, and C:N ratio.

Seed composition and contents of carbohydrates, protein, oil, and mineral nutrients, their interactions, and relationships with the physiological, agronomic, and nutritional characteristics, especially under stress, have been the subject of many reviews (e.g., Welch and Graham, 2005). Peterson et al. (2005) emphasized the need to maximize grain nutrient quality in relation to yield, especially under biotic and abiotic stress conditions. Nutrient densities have positive and negative correlations with protein and groat weight of oat, respectively (Peterson et al., 1975); however, when the state of balance among nutrients is disrupted by stress, their antagonistic interactions are reflected on reduced grain yield (Fageria, 2001). Results of a previous study (Riedell et al., 2007), showed that spring wheat and oat exhibited

temporally variable physiological and agronomic responses to a number of biotic stresses caused by aphid feeding or by aphid-vectored virus. The objective of this follow-up study was to quantify the complex interactions of nutrient densities, and C:N ratio in leaves, kernels and groats of oat subjected to biotic stresses and their effects on its grain yield, yield components, and grain composition during two years of contrasting rainfall and temperature regimes.

MATERIALS AND METHODS

Detailed information on the experimental design, aphid infection and plant sampling are available in Riedell et al. (2007). The following is a brief description for the purpose of this part of the study. A two-year (1997 and 1998) field experiment conducted at the Eastern South Dakota Soil and Water Research Farm (44° 19′ N, 96° 44′ W, and 500 m altitude) in a randomized complete block design with three replicates and a 4 Mg ha^{-1} yield target, was designed to test the impact of aphid feeding or aphid-vectored virus infection on the oat (*Avena sativa* L.) variety "Jerry."

Infection by bird cherry-oat (BCO) aphid (*Rhopalosiphum padi* L.), green bug (GB) (*Schizaphis graminum* Rondani) and Russian wheat aphid (RWA) (*Diuraphis noxia* Mordvilko), and aphid-vectored virus (barley yellow dwarf virus, BYD) was carried out as described in Riedell et al. (2007). Check (CHK) plots were included in all replicates. Plants were sampled at the boot and early heading stages after aphid infestation, and the following were recorded on sampled plants or on whole plots: leaf area index (LAI) on plot basis using LAI-2000 crop canopy analyzer, and number of leaves, leaf area and tillers per plant in a 30-cm section in a middle row of each plot and replicate. Midday differential canopy temperature was calculated from temperature readings using an infrared thermometer on whole plots taken prior to plant sampling. The dT values reflect an inverse relationship between canopy temperature and transpiration cooling (Jackson et al., 1982); larger dT values indicate reduced plant capability to meet transpiration cooling. Percent groat, a "packaging cost" (expressed as hull/kernel weight ratio), nutrient densities, C:N ratios, protein, and oil contents were based on archived seed samples. Nitrogen use efficiency (NUE; g GY g^{-1} N), and nitrogen harvest index (NHI; the ratio of grain N content to shoot N content at maturity) were calculated according to Peterson and Rendig (2001).

Determination of Nutrients, C:N Ratio, Protein and Oil Content

Plant samples were dried at 45°C in a forced air oven for a one week period or until no further reduction in weight occurred. Kernels and groats were ground then placed through a 1 mm screen while leaf tissues were processed as described in Riedell et al. (2007). Digestion of plant materials

followed the US-EPA 5051 method. A 0.5 g sample weight was digested with 6.5 mL nitric acid. Chemical analysis was completed using the Varian Vista-Pro CCD (Charge Coupled Device, Varian Incorporated, Hansen Way, Palo Alto, CA, USA) Simultaneous inductively coupled plasma (ICP)-Optical Emission Spectroscopy (OES) instrument. MNUSDA-STD 1-A and MNUSDA-STD 2 (Inorganic Ventures, Lakewood, NJ, USA) were prepared as elemental standards. Carbon and nitrogen were determined on sub-samples using a LECO FP-428 analyzer (LECO, St. Joseph, MI, USA). Nitrogen was converted to protein by multiplying by 6.25. Sub-samples of groats were extracted with petroleum followed by gravimetric analysis for oil content determination.

Statistical Analyses

Data collected during two cropping seasons were tested for homogeneity of variances and, if needed, to transform data in order to satisfy multivariate analyses assumptions prior to statistical analyses. Nutrient densities were log-transformed prior to statistical analyses, then back-transformed for reporting (StatSoft Inc., 2008b). Total variance in each dependent variable explained by differences among years, stress treatments, and their interaction using the restricted maximum likelihood method (REML) was calculated and tested for significance, with stress treatments and years as fixed and random factors, respectively. A whole model R^2 was calculated for each dependent variable and was partitioned according to its sources of variation (Payne et al., 2007).

The Partial Least Squares (PLS) regression option in the Non-linear Iterative Partial Least Squares (NIPALS) algorithm (Esbensen, 2005; Camo ASA, 2007) was used on the raw data to construct a set of components that accounts for as much variation as possible while modelling 1) dT as a function of plant architectural components; 2) C:N as a function of nutrient densities in leaves, kernels, and groats and separately for each stress treatment; 3) kernel weight, kernels m^{-1}, and GY as functions of dT; 4) kernels m^{-1}, and GY as functions of C:N ratio in kernels; and 5) protein content in leaves, kernels and groats as function of nutrient densities.

Comparison of the regression lines calculated for 1997 and 1998 verified that both the slope and intercept values were not significantly different ($LSD_{0.1}$) for the two years (StatSoft Inc., 2008b). The PLS models developed in this analysis were cross-validated by successively leaving out data one at a time. A model was built using the remaining data points then the model created was used to predict the dependent variable (Esbensen, 2005). Canonical correlation was performed to examine the impact of years, stress treatments and clusters of the year-stress combinations (based on grain yield and its components) on the multivariate relationships between nutrient densities and C:N ratios in leaves, kernels and groats.

Principal components analysis (PCA), a dimension reduction and perceptual mapping statistical procedure (StatSoft Inc., 2008a), was employed to reduce the dimensionality of a matrix based on all factors (years and stress treatments) and variables (plant architectural components, dT, chlorophyll, C:N ratio, nutrient densities, protein, oil, kernel weight, kernels m^{-1}, and GY) in the data set of leaves, kernels and groats separately. The temporal relationships between nutrients in leaves, kernels and groats, and the cumulative variance (multiple R^2) for each nutrient were developed to test whether a unique rate-limiting process was caused by the stress treatments. The 10 combinations of year-stress treatments were tested for differences in their GY and its components; three clusters, significantly different for these variables were identified and included in the multivariate analyses.

RESULTS

Variation in Agronomic and Nutrient Traits

Overall means and coefficients of variation (C.V.) of agronomic and nutrient-related traits in oat subjected to biotic stresses during two years of contrasting rainfall and temperature regimes (Table 1) indicate significant

TABLE 1 Overall means, mean separation, and coefficients of variation (C.V.) of agronomic and nutrient-related traits in oat subjected to biotic stresses during two years of contrasting rainfall and temperature regimes. NHI (Nitrogen harvest index,%) NUE (Nitrogen use efficiency, g $GY\,g^{-1}$ N; protein (calculated as N × 6.25), and oil contents are in g kg^{-1}; and nutrient densities are in mg g^{-1}

| Agronomic traits | | | | Nutrients in | | | | | |
| | | | | Leaves | | Kernels | | Groats | |
A Variable	Mean	C.V.	B Variable	Mean	C.V.	Mean	C.V.	Mean	C.V.
Grain yield	4.03*[†]	25	C:N ratio	23.6a[§]	9	19.6b	6	14.5c	4
Kernels m^{-1}	596.00*	30	Protein	178a	15	180a	6	136b	4
TKWT, g	31.40*	15							
Groat%	73	6	Nutrients	36.4a	14	12.8b	7	11.9b	8
Packaging cost	27*	10							
dT °C	4.10*	34	Ca	6.2a	12	0.56b	16	0.74b	18
Leaves/plant	8.40*	26	Cu	0.007	15	0.006	35	0.005	20
LAI	2.40*	35	Fe	0.115a	43	0.059b	10	0.055b	22
Tillers/plant	1.80*	34	K	23.7a	18	3.8b	10	4.4b	20
LA/plant cm^2	96.60*	25	Mg	2.8a	20	1.47b	7	1.33b	8
Chl. mg g^{-1}	10.50*	20	Mn	0.054	40	0.052	14	0.052	10
Chl:N ratio	0.33*	16	P	1.7b	45	4.6a	12	3.53a	10
NHI,%	45*	20	S	1.76	40	2.2	6	1.79	6
NUE	25.2*	24	Zn	0.02b	20	0.039a	23	0.035a	20
Oil g kg^{-1}	79*	12							

[†]*, Significant differences ($P < 0.05$) between means of the 10 combinations of year-stress treatments.
[§]Means of each variable followed by different letters differ significantly (Tukey's HSD, $P < 0.05$).

differences in agronomic traits between the 10 combinations of year-stress treatments (Table 1A) and wide variation in most traits as measured by coefficients of variation (C.V.). In spite of the negative impact of biotic and abiotic stresses, mean grain yield (GY) was on the target of 4.0 Mg ha^{-1}; however, GY, as well as most other agronomic traits, were associated with a relatively large C.V. (25%). All agronomic traits, except percent groat, were significantly impacted by stress treatments during both years. Significant differences were found between leaves, kernels and groats for all nutrient-related traits, except for densities of copper (Cu), and manganese (Mn) (i.e., [Cu] and [Mn]) (Table 1B). A general decreasing trend was observed in the level of variation in the nutrient-related traits, including C:N ratio and protein content, as the nutrients were remobilized from leaves to kernels and then to groats. However, Ca was an exception; its C.V. increased slightly from 12% in leaves to 18% in groats. Nutrients displayed larger and wider range of variation in leaves (12–45%), as compared to kernels (6–35%) or groats (6–22%). Total nutrients density dropped by 33% as nutrients were remobilized from leaves to groats mainly due to a sharp decline in calcium (Ca), iron (Fe), potassium (K), and magnesium (Mg). Densities of the remaining nutrients, either slightly increased [phosphorus (P) and zinc (Zn)] or remained relatively stable [Cu, Mn, and sulphur (S)].

Grain yield and yield components of three clusters identified in the 10 combinations of year-stress treatments were significantly different (data not presented). The first and second clusters were comprised of all stress treatments in 1997, and 1998, respectively, except BYD-infected plants in both years, which constituted the third cluster. The oat crops in Cluster 1 significantly produced more GY (4.75 Mg ha^{-1}), more kernels m^{-1} (760) and heavier kernels (34.2 mg kernel^{-1}) than the oat crops in Cluster 2 (3.96 Mg ha^{-1}, 505 kernels m^{-1}, and 27.2 mg kernel^{-1}). The oat crops in Cluster 3 produced significantly less GY (2.73 Mg ha^{-1}) due to significantly fewer (440) kernels m^{-1}, and a kernel weight (34.3 mg) similar to that of Cluster 1. In addition, plants in Cluster 3 had significantly smaller average chlorophyll content (7.96), as compared to the CHK (11.44 mg g^{-1}).

Stress Impact on Agronomic and Nutrient Traits

Significant ($P < 0.05$) percent variances explained by years, stress treatments and their interaction in each of the architectural components, grain-related traits, nutrients and C:N ratios are presented in Table 2. Architectural components were largely impacted by years and years x stress treatments interaction. However, chlorophyll (Chl) content, Chl:N ratio and nutrients in leaves were impacted by all three sources of variation; whereas, a sizable portion (0.68) of the variance in each of nitrogen use efficiency (NUE) and nitrogen harvest index (NHI) was explained largely by differences between stress treatments. The NUE averaged 25.2 and ranged from 17.0 for BYD to

TABLE 2 Significant ($P < 0.05$) percent variance explained by years, stress treatments and their interaction in grain-related traits and nutrients, and C:N ratio in leaves, kernels and groats of oat subjected to biotic stresses caused by aphid feeding or by aphid-vectored virus during two years (1997 and 1998) of contrasting rainfall and temperature regimes.

| | Percent variance ($P < 0.05$) due to: | | | |
Variable	Years	Stress treatments	Years x Treatments	R^2
Leaf area per plant	14		48	0.54
Number of leaves per plant			30	0.22
Number of tillers per plant	18		47	0.57
Leaf area index (LAI)	70		28	0.89
Chlorophyll content (Chl)	37	23	25	0.78
Chlorophyll: Nitrogen ratio (Chl:N)	44	8	37	0.84
Nutrients in leaves	10	37	7	0.48
C:N ratio in leaves	67			0.57
Midday differential canopy temperature	76		14	0.78
Nutrients in kernels	41	6	6	0.40
Nutrients in groats	47	10	12	0.70
C:N ratio in kernels	72			0.58
C:N ratio in groats	57			0.57
Kernels m^{-1}	67	15		0.83
Thousand-kernel weight	86	10		0.94
Percent groat	77	12		0.87
Packaging cost	80	7		0.77
Protein in kernels	53		8	0.54
Nitrogen use efficiency, NUE (g GY g^{-1} N)	10	59		0.68
Nitrogen Harvest Index, NHI	18	50		0.68
Oil in kernels		58		0.67
Grain yield, (GY)	23	46	6	0.76

29.8 g GY g^{-1} N for the CHK; whereas, NHI averaged 45 and ranged from 32 for BYD to 53% for the CHK.

Large variances ($R^2 > 0.76$) associated with grain-related traits were explained mostly by temporal variation and, to some extent, by stress treatments, whereas the relatively large variance associated with dT (0.76) was explained only by temporal variation. In comparison, smaller variances associated with protein (0.54) and oil (0.67) contents were explained by temporal variation and stress treatments, respectively. Temporal variation accounted for 0.37 of the variance associated with nutrients in leaves, whereas stress treatments accounted for the largest variances associated with nutrients in kernels (0.41) and groats (0.47). The year x stress treatment interaction accounted for smaller variances in all three variables.

Percent variance associated with nutrients and explained by temporal variation increased during plant ontogeny from 10% (nutrients in leaves) to 47% (nutrients in groats); whereas, the opposite was found for percent variance explained by stress treatments. The C:N ratios had 57–72% of their variances explained by temporal variation only. Significant variances

explained by the year x stress treatment interaction ranged in magnitude from 6 to 48%; the largest (25–48%) were associated with plant architectural components, chlorophyll content and Chl:N ratio; whereas the smallest (<14%) were associated with GY, protein, and nutrients in leaves, kernels and groats.

Discrimination between Stress Treatments

The 10 combinations of year-stress treatments were 100% correctly classified based on variables included in the canonical discriminant analysis (Figure 1). Two canonical discriminant functions (CAN1 and CAN2) accounted for 92% of total variance and were derived from agronomic and nutrient-related traits. CAN1 accounted for 75% of total variance, with large loadings of nutrients in kernels, GY, kernels m^{-1}, and LAI, and totally separated the 1997 from 1998 stress treatments. CAN2 accounted for a significant, but smaller portion (17%) of total variance with large loadings of nutrients in leaves and groats, TKWT, dT and hull, and separated four stress treatments (BYD7, BCO7, BYD8, and CHK8) from the rest.
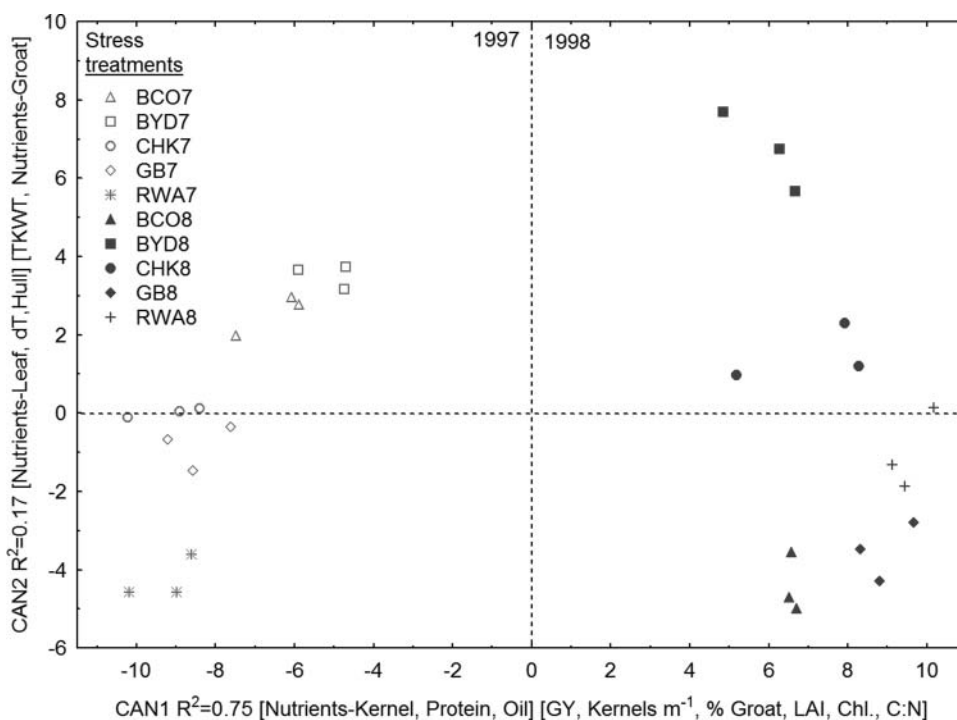

FIGURE 1 Discriminant analysis based on agronomic and nutrient-related traits among oat plants subjected to biotic stresses caused by aphid feeding or by aphid-vectored virus during two years of contrasting rainfall and temperature regimes.

Plants subjected to stress treatments during 1998 (Cluster 1) were associated with smaller [Ca], [K], and [N], and larger C:N ratios and densities of the remaining nutrients in their leaves as compared to those in Cluster 2; whereas, plants in Cluster 2 were associated with smaller values for all nutrient densities and C:N ratio in their leaves and kernels as compared to plants in Cluster 1. Plants infected with BYD virus (Cluster 3) responded to temporal variation in a different manner and that was reflected on their significantly smaller GY, and fewer kernels m^{-1}, but larger kernel weight as compared to plants in Cluster 2.

Multivariate Relationships between Variables

A strong canonical correlation (Figure 2) was found between agronomic and nutrient-related traits ($R^2 = 0.92$; $P < 0.0001$), with 68 and 62% total redundancies, respectively. CAN1, extracted from the agronomic traits data set accounted for 48% of their total variance, whereas CAN1 extracted from the nutrient-related traits accounted for 42% of their total variance. Stress treatments were separated at the origin (i.e., 0.0, 0.0) of both canonical functions, with a slightly wider spread of the 1997 on CAN1 of nutrient-related traits as compared to the 1998 stress treatments.

Nutrient densities and C:N ratio in leaves were strongly associated with those in kernels as indicated by the large and significant canonical R^2 value
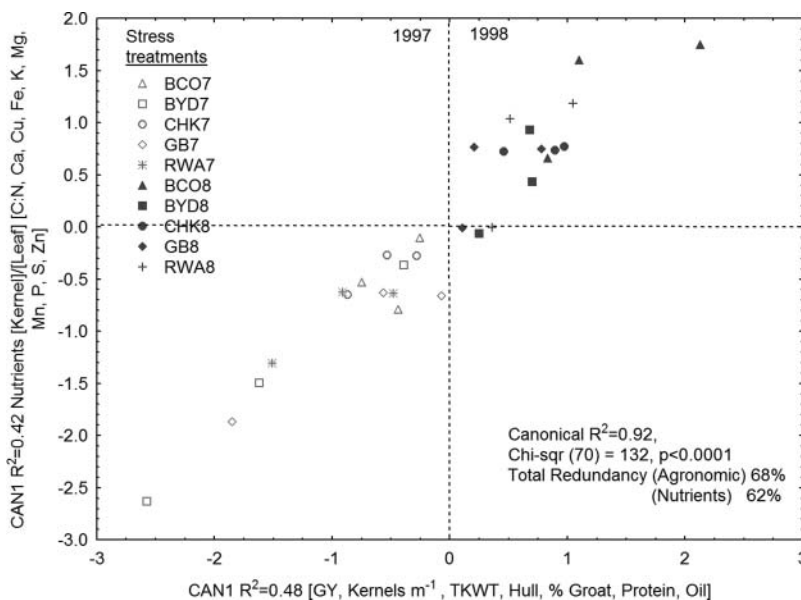

FIGURE 2 Canonical correlation between agronomic and nutrient-related traits in oat plants subjected to biotic stresses caused by aphid feeding or by aphid-vectored virus during two years of contrasting rainfall and temperature regimes.
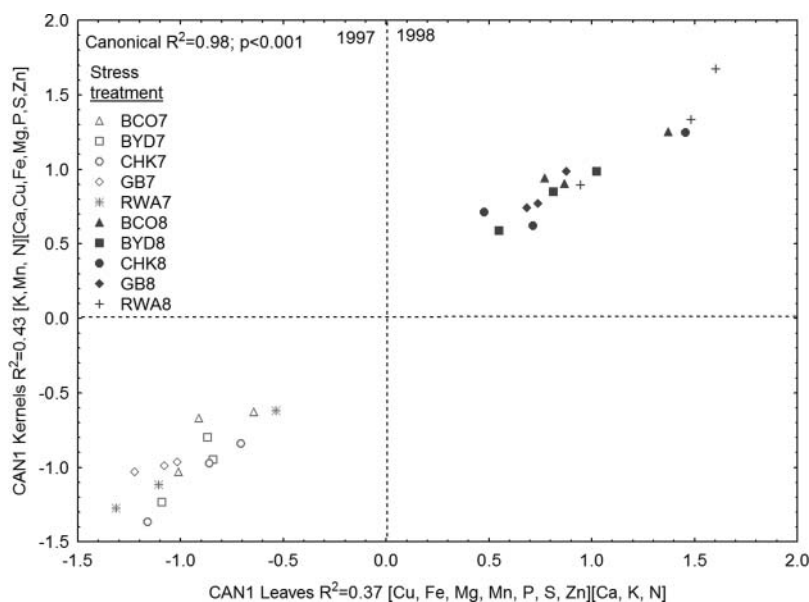
FIGURE 3 Loadings on and variance explained by the first canonical functions, correlation between nutrients in leaves and kernels of oat subjected to biotic stress treatments caused by aphid feeding or by aphid-vectored virus during two years of contrasting rainfall and temperature regimes.

of 0.98 (Figure 3). The first canonical function derived from C:N ratio and nutrient densities in leaves accounted for 0.37 of the variance; whereas, the respective value for nutrient densities in kernels was 0.43. The 1997 and 1998 stress-treatment combinations were totally separated at the origin of both canonical functions. Three nutrients in leaves (Ca, K, and N) have positive loadings; whereas the remaining nutrients (Cu, Fe, Mg, Mn, P, S, and Zn) have negative loadings on CAN1. A slightly different loading pattern on CAN1 was observed for nutrient densities in kernels; K, Mn, and N loaded negatively; whereas, the remaining nutrients (Ca, Cu, Fe, Mg, P, S, and Zn) loaded positively on CAN1. Percent significant pairwise correlation (PSPC) coefficients between nutrients in leaves, kernels and groats were 50, 75 and 50, respectively. The r-values were within the range of |0.39 to 0.87| in leaves, |0.38 to 0.89| in kernels and |0.36 to 0.60| in groats. When averaged over years, the largest (75%) PSPCs were found for the CHK and GB, the smallest (50%) for BCO and BYD, and the intermediate (60%) for RWA plants (data not presented).

Total nutrient densities in leaves, kernels and groats and their ratios (Table 3) exhibited diverse, positive and negative relationships with grain yield and its components, and with protein and oil contents. Among the significant ($P < 0.05$) correlation coefficients in Table 3, the negative (-0.42) and positive (0.68) r-values between TKWT and each of nutrient densities in leaves and groats, respectively, are of particular significance. The ratio

TABLE 3 Significant ($P < 0.05$) correlation coefficients between agronomic- and nutrient-related traits in oat plants subjected to biotic stresses during two years of contrasting rainfall and temperature regimes

Group	Variable	GY	K m^{-1}	TKWT	Percent groat	Packaging cost	Protein	Oil
				Significant ($P < 0.05$) correlation coefficients				
Nutrients in								
	Leaves	0.55		−0.42				
	Kernels	−0.45	−0.55		−0.45	0.45	0.51	0.37
	Groats	−0.40		0.68	0.43	−0.43		
Nutrient density ratio[†]								
	[K]/[L]	−0.67	−0.53					
	[G]/[K]			0.81	0.67	−0.80	−0.38	−0.35
C:N ratio in								
	Leaves	0.65	0.79	0.49	0.50	−0.58	−0.73	−0.53
	Kernels	0.72	0.83	0.46	0.54	−0.64	−0.88	−0.42
	Groats	0.72	0.83	0.44	0.55	−0.57	−0.93	−0.54
	Chlorophyll	0.66	0.69					
	dT	−0.50	−0.70	−0.60	−0.55		0.54	0.43
	LAI	0.51	0.79	0.81	0.77	−0.77	−0.64	−0.58

[†], [L], [K], and [G]: total nutrients density in leaf, kernel and groat, respectively.

of nutrient density in kernels/leaves (i.e., [K]/[L]) was negatively correlated with GY and with kernels m^{-1}; whereas, the ratio of nutrient density in groats/kernels (i.e., [G]/[K]) was positively correlated with TKWT and with percent groat, and negatively correlated with packaging cost, and with protein and oil contents. Grain yield and its components were positively correlated with the C:N ratios in leaves, kernels and groats; however, protein and oil contents were negatively correlated with the C:N ratios. Finally, chlorophyll was correlated with GY and kernels m^{-1}; whereas dT and LAI displayed opposite relationships with grain yield and its components. During the stress year (1997), chlorophyll was correlated ($P < 0.05$) with: [Fe] in leaves ($r = 0.34$), dT ($r = −0.48$), and leaf area per plant ($r = 0.59$) at the boot stage. During the non-stress year (1998), the chlorophyll content in leaves was independent of [Fe], the correlation with dT became stronger ($r = −0.73$), the correlation with leaf area per plant remained significant ($r = 0.37$), and the correlations with LAI (0.44), number of leaves (0.47) and tillers (0.59) per plant were significant ($P < 0.05$).

Modeling dT as a Function of Architectural Components

Midday differential canopy temperature (dT) estimation, whether for individual or all stress treatments was reliable ($Q^2 > 0.80$), except BCO, which unlike other treatments, had a non-significant model intercept (β_o) (Table 4). When dT was estimated for all treatments combined, all partial regression coefficients (β) were negative and the two non-significant β's were those of number of leaves (β_2) and leaf area (β_4) per plant (Table 4).

TABLE 4 Validation PLS regression models, their statistics, and level of significance of explained variance in midday differential canopy temperature as a function of leaf area index (LAI), number of leaves per plant, number of tillers per plant and leaf area per plant, in oat subjected to biotic stresses caused by aphid feeding or by aphid-vectored virus during two years (1997 and 1998) of contrasting rainfall and temperature regimes

Treatment/Cluster	Q^2	Model β_o	LAI, β_1	Leaves/ plant, β_2	Tillers/ plant, β_3	Leaf area/ plant, β_4
All treatments	0.80*†	9.05*	−1.30*	−0.10	−0.46*	−0.002
Cluster 1 (1998)	0.75*	8.50*	−1.10*	−0.53*	0.34	0.012*
Cluster 2 (1997)	0.53*	8.20*	0.20	0.90*	−6.40*	−0.020
Cluster 3 (BYD 1997, 1998)	0.83*	9.70*	−1.20*	−0.25	2.24	−0.040*
Check (CHK)	0.97*	12.40*	−2.97*	−0.77*	4.50	−0.023
Bird-cherry oat aphid (BCO)	0.62	1.63	0.62	0.55	−4.70	0.044
Barley yellow dwarf virus (BYD)	0.83*	9.70*	−1.20*	−0.25	2.24	−0.040*
Green bug (GB)	0.89*	10.70*	−2.21*	−0.50*	1.30	−0.002
Russian wheat aphid (RWA)	0.95*	7.30*	−1.18*	0.32*	−1.80*	0.010*

†*, validation Q^2 value is significant at $P < 0.05$ (Tukey's, HSD).

A larger error variance was associated with dT estimates during the stress (1997) as compared to the non-stress year (1998). LAI and number of leaves per plant had negative and significant impact on dT estimates during the non-stress year; whereas, tillers and leaf area per plant had negative and significant impact on dT during the stress year. Estimates of dT for BYD-infected plants were negatively impacted by all architectural components, except tillers per plant.

The individual plant architectural components differed in their magnitude and significance in predicting dT when individual stress treatments were considered. Reliability of dT estimates for the non-stress (CHK) and the BCO treatments were the largest ($Q^2 = 0.97$) and smallest ($Q^2 = 0.62$), respectively. Architectural components of the GB-infected plants impacted dT estimation in the same manner as those of the CHK. All four architectural components in RWA-infected plants contributed significantly to predicting dT with large reliability ($Q^2 = 0.95$); larger number of leaves and leaf area per plant, and smaller LAI and fewer tillers per plant led to larger and smaller dT values, respectively.

Modeling GY and its Components as Functions of dT

The validation PLS models for kernel weight [$-1.73(dT)+38.6$, r = -0.60, $P < 0.001$], number of kernels m^{-1} [$-83.3(dT)+938$, r = -0.69, $P < 0.001$], and GY [$-0.34(dT)+5.43$, r = -0.50, $P < 0.001$] as functions of dT for all stress treatments combined and during both years had the respective small but significant validation Q^2 values of 0.36, 0.48 and 0.25. On average, kernel weight, number of kernels m^{-1}, and GY would decrease by 1.73 mg, 83.3 kernels m^{-1}, and 0.34 Mg ha^{-1} with each increase of one

TABLE 5 Validation PLS regression models of kernel weight (mg), number of kernels m^{-1}, and grain yield (Mg ha^{-1}), as functions of midday differential canopy temperature (dT) in oat subjected to biotic stresses caused by aphid feeding or by aphid-vectored virus during two years (1997 and 1998) of contrasting rainfall and temperature regimes.

Treatment/ Cluster	Dependent variable	R^2	Model β_o	Regression coefficient, β
	Kernel weight			
Cluster 1 (1998)		0.30*†	31.5	0.97
Cluster 2 (1997)		0.03	26.0	0.23
Cluster 3 (BYD)		0.66*	49.3	−3.19
	Kernel weight			
CHK		0.59*	36.6	−1.85
BCO		0.19*	36.2	−1.10
BYD		0.66*	49.3	−3.19
GB		0.56*	41.2	−2.84
RWA		0.96*	40.7	−2.26
	Kernels m^{-1}			
CHK		0.61*	983.0	−82.9
BCO		0.31*	985.0	−82.4
BYD		0.55*	831.0	−81.8
GB		0.29*	691.0	−34.6
RWA		0.85*	1050.0	−92.6
	Grain yield, Mg ha^{-1}			
CHK		0.47*	5.9	−0.29
BCO		0.25*	5.9	−0.39
BYD		0.38*	3.9	−0.25
GB		0.35*	3.5	−0.11
RWA		0.65*	5.8	−0.33

†*, significant at $P < 0.05$ (Tukey's, HSD).

$^{\circ}$C dT. Nevertheless, when individual stress treatments were considered, the validation models for kernel weight, number of kernels m^{-1}, and GY displayed a wide range of variances (i.e., Q^2) explained by differences in dT (Table 5). Additionally, the largest error variances were invariably associated with BCO and the smallest with RWA; whereas, error variances associated with the CHK were intermediate.

Regression coefficients indicate that BCO- and BYD-infected plants would lose the least (1.1 mg) and the most (3.19 mg) weight per kernel with each increase of one $^{\circ}$C dT; whereas, number of kernels m^{-1} in the RWA- and GB-infected plants would be reduced by 34.6 and 92.6, respectively. Number of kernels m^{-1} for the remaining treatments (i.e., BCO- and BYD-infected plants), in addition to the CHK, would be reduced by ∼82 kernels with each increase of one $^{\circ}$C dT. A similar trend was found for GY; GB- and BCO-infected plants are predicted to lose the least (0.11 Mg ha^{-1}) and the most (0.39 Mg ha^{-1}) grain yield with each increase of one dT $^{\circ}$C, respectively. All Q^2 values were significant except for kernel weight estimate in Cluster 2 (i.e., during the stress year). Moreover, dT failed to reliably predict kernels m^{-1} or GY in all Clusters.

Modeling C:N Ratios as Function of Nutrient Densities

The C:N ratio for the whole data set was estimated as a function of nutrient densities using PLS regression with large reliability (Model $\beta_o = 7.25$, validation $Q^2 = 0.70$, RMSE $= 2.06$); all nutrients, except K and Zn, had significant positive impact on C:N estimates. When C:N ratios in leaves, kernels and groats were estimated separately, the resulting PLS regression models differed significantly from each other as follows:

$$\text{C:N in Leaves} = 19.7 + 0.06\,(\text{Fe}) + 0.79\,(\text{Mg}) + 0.028\,(\text{Mn}) + 0.44\,(\text{P})$$
$$+ 0.61\,(\text{S}) + 0.005\,(\text{Zn}); (Q^2 = 0.34;\ \text{RMSE} = 1.2) \quad (1)$$

$$\text{C:N in Kernels} = 24.9 - 0.8\,(\text{Ca}) - 0.02\,(\text{Cu}) + 0.08\,(\text{Mn}) - 1.7\,(\text{P});$$
$$(Q^2 = 0.31;\ \text{RMSE} = 1.2) \quad (2)$$

$$\text{C:N in Groats} = 17.8 - 0.4\,(\text{Ca}) - 0.004\,(\text{Cu}) + 0.25\,(\text{K}) + 0.02\,(\text{Mn})$$
$$- 1.1\,(\text{P}) - 0.023\,(\text{Zn});\ (Q^2 = 0.49;$$
$$\text{RMSE} = 0.48) \quad (3)$$

Similarly, stress treatments differed as to the statistics of their validation PLS models (i.e., Model β_o, Q^2, and RMSE), and the nutrients contributing significantly to the C:N estimation, as follows:

$$\text{C:N in CHK: Model } \beta_o = 5.6;\ Q^2 = 0.70;\ \text{RMSE} = 2.2,$$
$$(\text{Cu, Fe, Mg, Mn, P, S}) \quad (4)$$

$$\text{C:N in BYD: Model } \beta_o = 11.6;\ Q^2 = 0.58;\ \text{RMSE} = 2.4,$$
$$(\text{Ca, Fe}) \quad (5)$$

$$\text{C:N in BCO: Model } \beta_o = 16;\ Q^2 = 0.54;\ \text{RMSE} = 2.6,$$
$$(\text{Ca, K, Mg, }-\text{P, }-\text{Zn}) \quad (6)$$

$$\text{C:N in GB: Model } \beta_o = 3.3;\ Q^2 = 0.75;\ \text{RMSE} = 1.8,\ (\text{K, P}) \quad (7)$$

$$\text{C:N in RWA: Model } \beta_o = 1.1;\ Q^2 = 0.85;\ \text{RMSE} = 1.5,$$
$$(\text{Cu, Fe, K, Mg, Mn, P, S}) \quad (8)$$

Modeling GY and Kernels m^{-1} as Functions of C:N Ratio

Mean separation and predictive models of kernels m^{-1} (Figure 4A) and grain yield (Figure 4B) as functions of C:N ratio in the groats of oat plants subjected to biotic stresses indicate that C:N ratio had a significant and positive impact on both dependent variables, but not on kernel weight (data not presented). On average, C:N ratio (Figure 4A) ranged from 13.63 to
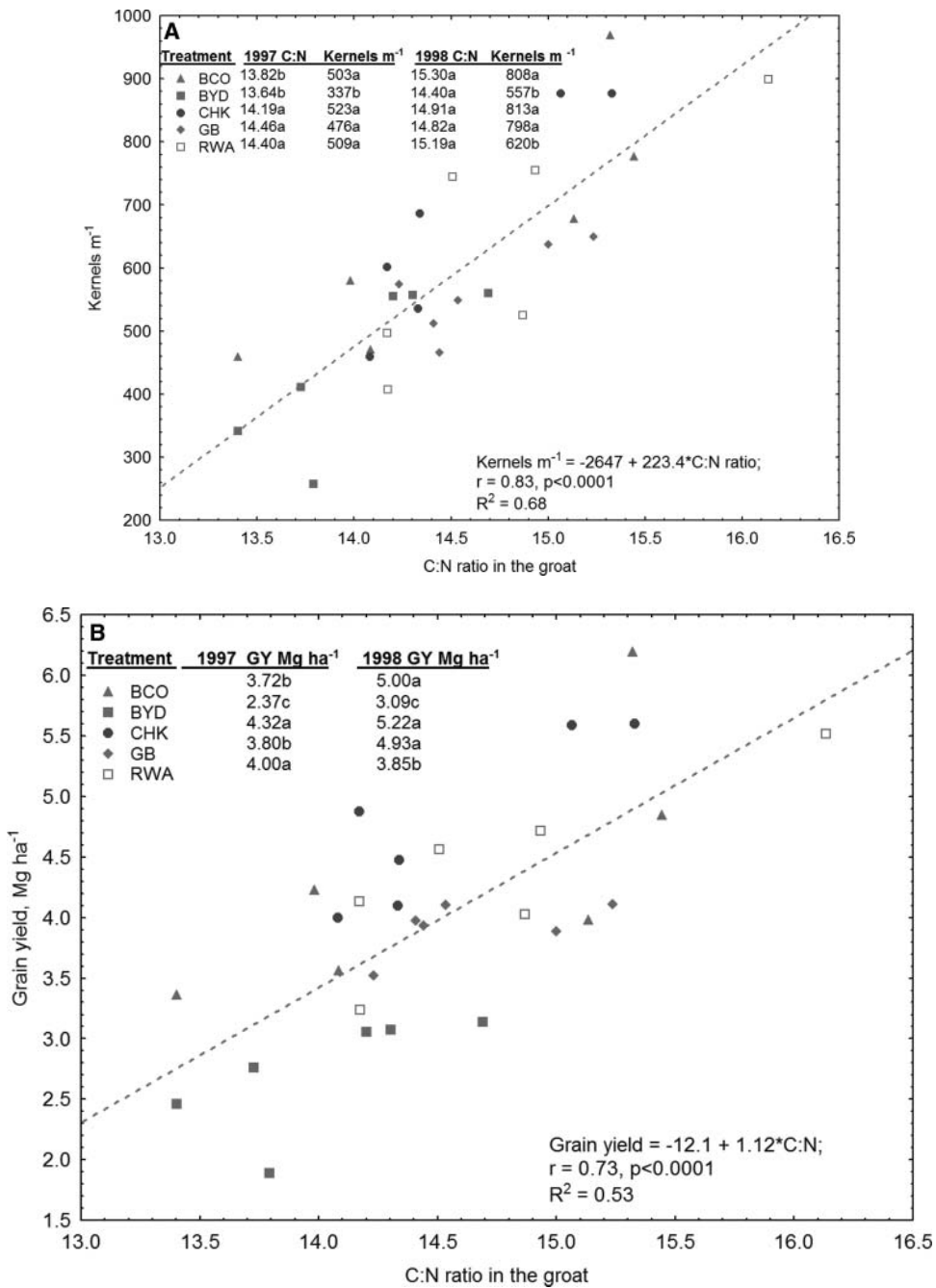
FIGURE 4 Mean separation (Tukey's HSD; $P < 0.05$) and validation PLS regression models of (A) kernels m^{-1}, and (B) grain yield as functions of C:N ratio in groats of oat subjected to biotic stresses caused by aphid feeding or by aphid-vectored virus during two years of contrasting rainfall and temperature regimes.

14.46 in 1997, and from 14.4 to 15.3 in 1998. Stress treatments differed significantly in their C:N ratios within (Tukey's HSD; $P < 0.05$) and between (t-test, $P < 0.05$) years. Significant differences in kernels m^{-1} in 1997 were found only between BYD and the remaining stress treatments, and in 1998, between each of BYD and RWA and the remaining stress treatments. The validation PLS model indicates that a large and significant variance in kernels m^{-1} ($Q^2 = 0.68$) was explained by C:N variation among stress treatments, and predicts that a unit increase in C:N ratio would result in an increase of about 223 kernels m^{-1}. A similar pattern was observed for GY and its response to C:N ratio (Figure 4B); however, with less, but significant variance ($Q^2 = 0.53$) in GY being explained by variation in C:N ratio. Mean GY estimates ranged from 2.37 (BYD) to 4.32 Mg ha^{-1} (CHK) in 1997, and from 3.09 (BYD) to 5.22 Mg ha^{-1} (CHK) in 1998. All stress treatments, except RWA, resulted in significantly smaller GY in 1997 as compared to 1998. The validation PLS model predicts that a unit increase in C:N ratio would result in an additional 1.12 Mg ha^{-1} in GY.

Modeling Protein Content as a Function of Nutrient Densities

Protein content (g kg^{-1}) in oat kernels was negatively correlated ($P < 0.05$) with C:N ratio in leaves (r = −0.53), kernels (r = −0.74) and groats (r = −0.95). These relationships impacted the reliability of estimating protein content as a function of nutrients in leaves, kernels, and groats of oat, as follows:

$$\text{Protein content in leaves} = 198 - 0.28(\text{Fe}) - 3.22(\text{Mg}) - 0.14(\text{Mn})$$
$$- 1.7(\text{P}) - 0.02(\text{Zn}); \ (Q^2 = 0.32; \ \text{RMSE} = 7.0);$$
$$\text{with C:N ratio, } R^2 = 0.54 \tag{9}$$

$$\text{Protein content in kernels} = 131 + 0.08(\text{Cu}) - 0.42(\text{Mn}) + 9.6(\text{P})$$
$$+ 0.5\text{Zn}; \ (Q^2 = 0.34; \ \text{RMSE} = 6.7);$$
$$\text{with C:N ratio, } R^2 = 0.55 \tag{10}$$

$$\text{Protein content in groats} = 143 + 4.2(\text{Ca}) + 0.04(\text{Cu}) - 2.8(\text{K})$$
$$+ 11.8(\text{P}) + 0.3(\text{Zn}); \ (Q^2 = 0.59; \ \text{RMSE} = 5.4);$$
$$\text{with C:N ratio, } R^2 = 0.85 \tag{11}$$

Temporal Variation and Nutrient Dynamics

Scatter plots, loadings, and variances explained by the first two validated principal components of plant architectural traits and nutrients

in leaves (Figure 5A), kernel- and yield-related traits (Figure 5B), and groat- and yield-related traits (Figure 5C), illustrate the temporal dynamics and interrelationships between all factors and variables in this study. The stress treatments were differentiated primarily along PC1; whereas each of
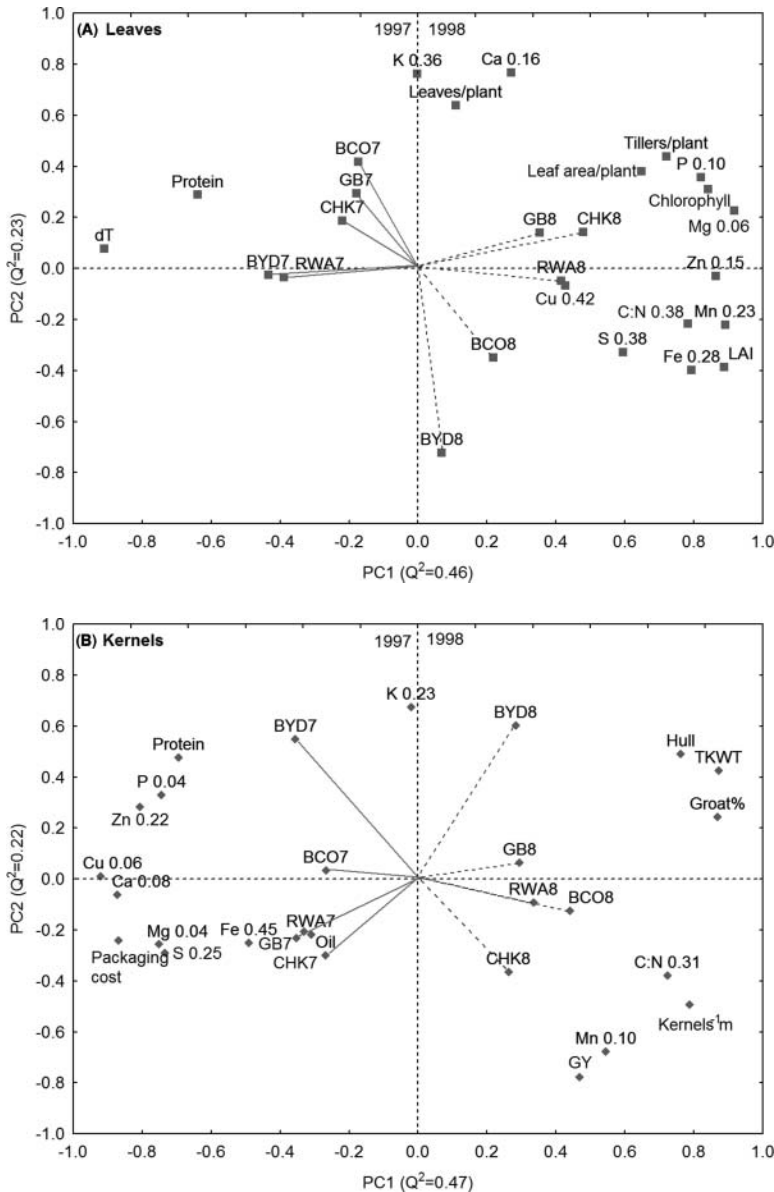
FIGURE 5 Variance explained by the first and second validated PCs, scatter plots, and loadings of plant architectural traits and nutrients in (A) leaves, (B) kernel and yield-related traits and (C) groat and yield-related traits of oat subjected to biotic stresses caused by aphid feeding or by aphid-vectored virus during two years of contrasting rainfall and temperature regimes (Unique variances, i.e., $1-R^2$ values, for nutrients and C: N ratio are listed next to their symbols). *(Continued)*
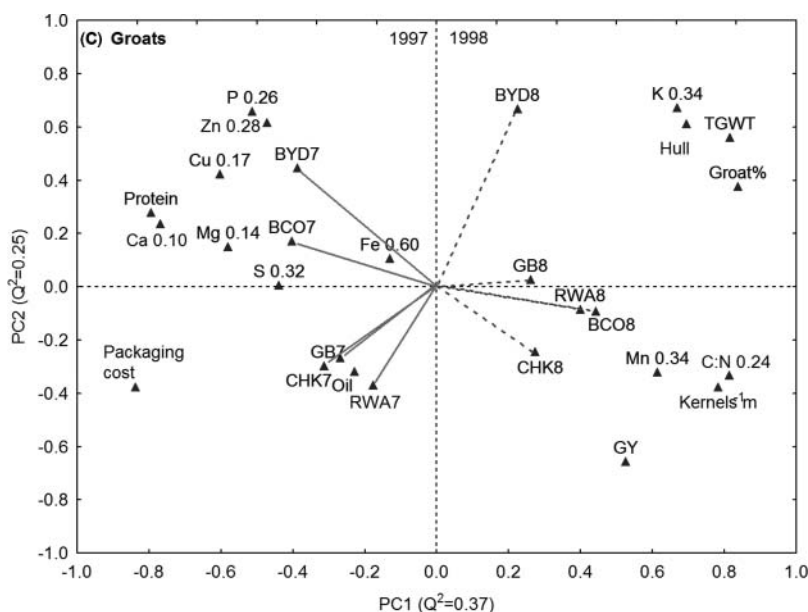
FIGURE 5 (Continued)

the plant-, kernel- and groat-related traits were differentiated more along PC2.

At the vegetative stage (Figure 5A), C:N ratio and most nutrients were associated with architectural components on PC1, which explained 0.46 of total variance, whereas, [Ca] and [K] were associated with leaves per plant on PC2, which explained additional 0.23 of total variance. Most nutrients exhibited large cumulative variances ($R^2 > 0.70$) with the exception of Cu (0.42), K (0.64) and S (0.62); these nutrients had large unique variances (i.e., $1-R^2$) as compared with other nutrients. The stress treatments that are plotted in the right and left quadrants generally have above and below average values for the variables in the same quadrants, respectively. For example, stress treatments in 1997 resulted in plants having larger leaf protein content and dT values as compared to the respective treatments in 1998. The BYD-infected plants, particularly in 1998 (i.e., BYD8), were deficient in Ca and K and developed fewer leaves per plant. The distance from the origin in Figure 5 (i.e., the 0,0 coordinates) is a general indication of the magnitude of the variable value above or below the mean of all stress treatments.

The PC analysis based on the kernel-related traits (Figure 5B) indicates that the stress treatments exhibited relatively slightly larger loadings in relation to PC1 (accounted for 0.47 of total variation) as compared to their loadings on PC1 of Figure 5A. Nutrient densities in kernels were differentiated by PC2 (which explained 0.22 of total variance), associated with oil and protein contents, and exhibited larger cumulative variances, except Fe, as

compared to nutrient densities in leaves. Most nutrients responded to stress treatments in different manners as indicated by their loadings on both PCs; however, K, with zero loading on PC1, and Ca and Cu, with zero loadings on PC2, responded to most stress treatments in the same manner.

Grain yield displayed a stronger and positive relationship with kernels m^{-1} than with TKWT, and a negative relationship with packaging cost, which, in turn, was inversely related to TKWT, percent groat and hull, and was larger for the smaller kernels produced in 1997 as compared to the heavier kernels produced in 1998. Protein and oil contents were differentiated from GY and yield components on PC1; however, they were negatively associated on PC2. Oil was associated with [Fe] and [S]; whereas, the protein content was associated with [Cu], [P] and [Zn].

Factors and variables in the PC analysis based on groat-related traits (Figure 5C) maintained relatively the same loadings on PC1, which accounted for 0.37 of total variance. Nutrient densities in groats were differentiated by PC2 (which explained 0.25 of total variance), associated with oil and protein contents, and exhibited slightly smaller cumulative variances as compared to nutrient densities in kernels. Most nutrients in groats responded to stress treatments with large positive or negative loadings on both PCs and with smaller cumulative variances as compared to nutrients in kernels; however, [Fe] and [S] exhibited smaller responses to almost all stress treatments in the same manner.

Cumulative nutrient variances in leaves, kernels and groats averaged 0.74, 0.84 and 0.72, respectively; therefore, the respective average unique nutrient variances ($1-R^2$) were 0.26, 0.16, and 0.28. Nutrients can be classified, as to their unique variances, into three categories. The first and second categories are comprised of nutrients with above-average (Fe, K, and S), and below-average (Ca, Mg, and P) unique variances in leaves, kernels and groats, respectively; whereas, the third category is comprised of nutrients with above-average unique variances in leaves, and below-average unique variances in kernels and groats (Cu, and Zn). Mn was the only nutrient with above-average unique variance in leaves and below-average in kernels and groats.

DISCUSSION

The diverse responses to biotic stresses during two years of contrasting growing conditions illustrate the complex interactions of plant architectural components, nutrient dynamics, and C:N ratio and their impact on grain yield and its components in oat. Abiotic stress can exacerbate the deleterious effects of aphid feeding (Riedell et al., 2007) and BYD virus infection (Persson et al., 2007) on the vegetative growth and grain yield of cereal crops, including oat. Very few traits (Table 2) had small error variance associated with them such like TKWT and percent groat; whereas, those having

a significant year x stress treatment interaction variance, especially the plant architectural traits, have large error variances (Peterson et al., 2005).

Plant architecture, in general, and the distribution and size of leaf area, in particular, are of fundamental importance to the acquisition and allocation of resources, to inter-plant competition (e.g., Villegas et al., 2007), and to stress tolerance (Kaitanieme et al., 1999). Biotic and abiotic stresses disrupted the nutrient relations and dynamics in oat plants, particularly through their effects on several plant architectural traits and chlorophyll content (Hu and Schmidhalter, 2005). The oat crop in this study was optimally supplied with N and other essential nutrients (Riedell et al., 2007); however, the large and significant variances in nutrient densities in leaves, kernels and groats can be attributed to the combined effects of temporal variation, stress treatments and their interaction (Table 2). Mean and C.V. values of NHI (45, 20%, respectively) and NUE (25.2 and 24%, respectively; Table 1) demonstrate the negative impact of biotic stress on these variables in the presence or absence of abiotic stress. Significantly larger NHI (48.0) and NUE (21.7 g dry weight g^{-1} N) were reported (Peterson and Rendig, 2001) for oat plants under fertilizer stress than non-stress conditions (36.0, and 16.6, respectively); whereas bread and durum wheat genotypes subjected to abiotic stress (low N fertilizer and late sowing date) or to no-stress (adequate N fertilizer and optimum sowing date) exhibited no significant differences between their respective NHI estimates of 71.0 and 69.2% (Ehdaie and Waines, 2001).

All four components of plant architecture (Table 2) displayed significant differences among stress treatments and had large (>25%) C.V. values, and explained large portions of the variance in dT (Table 4). Therefore, modifying plant architecture may lead to improved resource acquisition, and help predict plant reaction to biotic (Persson et al., 2007) and abiotic (Kaitanieme et al., 1999) stresses, if and when realistic models of plant architecture are developed.

By definition, C:N ratio is inversely related to, and can be reliably predicted by N, but not C or N+C content of plant material. The validation PLS regression models for C:N ratio as a function of nutrient densities explained significant, but small portions of variances of C:N ratio in leaves (0.34,), kernels (0.31), and groats (0.48). These Q^2 values are inversely related to the respective C:N ratios of 23.6, 19.6 and 14.5 (Table 1); a similar trend was found in five crops with diverse C:N ratios and chemical composition (Jaradat et al., 2008) suggesting that small C:N ratios can be predicted more accurately than large ones (Abiven et al., 2005). However, when individual biotic stress treatments were considered, the validation PLS models for C:N ratio as a function of nutrient density explained larger portion of its variation (range from 0.54 in BCO- to 0.85 for RWA-infected plants). Different nutrient combinations, as indicated by the validation PLS regression models, contributed to this discrepancy, and indicate that when the state of balance

among nutrients is disrupted by stress, their antagonistic interactions are reflected on the C:N ratio (Fageria, 2001) and on reduced grain yield. Nevertheless, C:N ratio was a better predictor of a yield component (kernels m^{-1}; $Q^2 = 0.68$) than GY itself ($Q^2 = 0.53$), and suggest that the smaller the amount of fixed carbon (e.g., BYD; Figure 4) the smaller the number of kernels m^{-1} and, consequently, the smaller the GY.

Crop plants usually react to biotic stresses by changing their photosynthetic rate due to alteration in the source-sink relationship. This is followed by chlorophyll breakdown as demonstrated in this study. BYD-infected plants lost 30% of the chlorophyll content compared to CHK, a value comparable to a 27% reduction in chlorophyll in rust- and mildew-infected wheat plants (Tartachnyk et al., 2006). The reduced vegetative growth, caused particularly by BYD infection, resulted in large [N] in leaves and in a concomitant decrease in chlorophyll content. These relationships are deduced from the loadings of BYD and plant architectural components on opposite sides of PC1 and PC2 (Figure 5A), and confirm earlier findings in oat (Persson et al., 2007).

Peterson et al. (2005) emphasized the need to maximize grain nutrient quality in relation to yield, especially under biotic and abiotic stresses. Nutrient densities have positive and negative correlations with protein and groat weight, respectively (Peterson et al., 1975); when the state of balance among nutrients is disrupted by stress, their antagonistic interactions are reflected on reduced grain yield (Fageria, 2001). Notwithstanding the large caloric input required for protein as compared to carbohydrate synthesis, the negative correlation between nutrient densities or protein content and groat weight found in this and other studies (e.g., Peterson et al., 2005) is probably due to the larger "packaging cost" found in smaller kernels (Table 3; Figure 5B and 5C). Packaging cost, as an investment in hull tissue that provides protection and nutrition to the embryo, may have contributed to kernel and groat weight variation as suggested by Grubb and Burslem (1998).

Nutrient interactions in crop plants, whether positive, negative or neutral, are probably among the most important factors affecting grain yield of cereal crops (Fageria, 2001). Total nutrient densities in leaves, kernels and groats and their ratios exhibited diverse, positive and negative relationships among themselves and with agronomic and yield-related traits. This level of association may reflect the presence of flexible and highly homeostatic mechanisms in support of nutrient uptake, accumulation, remobilization, and storage (Grusak et al., 1999) and in response to biotic and abiotic stresses (Persson et al., 2007).

Oat was reported (Fageria, 2001; Lombnæs and Singh, 2003) to be sensitive to Mn deficiency. A strong antagonistic relationship between Mn and most other nutrients, especially Fe and Zn, was reported in the literature (Fageria, 2001). This relationship was evident in oat leaves, kernels and groats (Figure 5), and can be attributed (Lombnæs and Singh, 2003;

Calderini and Ortiz-Monasterio, 2003) to the decline in biomass production under Mn deficiency. Manganese was the only nutrient, in this study, to maintain its positive and negative loadings on PC1 and PC2, respectively, whether in leaves, kernels or groats, and to maintain a largely positive relationship with plant architectural components, C:N ratio, grain yield and yield components. The [Fe]/[Mn] ratio (1.7) found in BYD-infected plants, although within the range of optimum values in most crop plants (1.5–3.0; Fageria, 2001) was larger than the one found for the check (1.4); similarly, it was larger during the stress year (1.6) as compared with the non-stress year (1.4).

Iron (Fe) showed different dynamics compared with other nutrients as indicated by its steadily increasing unique variance in leaves (0.28), kernels (0.45), and groats (0.60). Although Fe, K, and S had above-average unique variances, K and S, but not Fe, shared most of their variances (R^2 from 0.62 to 0.73) with other nutrients. This finding indirectly suggests that Fe differs from other nutrients (e.g., K, S, Cu, Mn, and Zn) in its unloading pattern into the developing grain (Calderini and Ortiz-Monasterio, 2003). Nutrients with above- or below-average unique variances (Figure 5) share very little, or most of their variances with other nutrients included in the analysis, respectively. This dynamism rules out the existence of a unique rate limiting process (Grusak et al., 1999) and confirms that wide differences exist in nutrient partitioning between oat leaves, kernels and groats when subjected to biotic and abiotic stresses.

We found an inverse relationship between TKWT and nutrient density in kernels (r = −0.4; $P < 0.05$), and a positive one between TGWT and nutrient density in groats (r = 0.7; $P < 0.001$). This discrepancy can be explained on the basis of the negative relationship between the packaging cost and each of nutrients in kernels (r = −0.43, $P < 0.01$), and TKWT (r = −0.88, $P < 0.001$). The allocation to "packaging cost" *senso lato* is usually significantly greater in smaller seeds (Grubb and Burslem, 1998) as was demonstrated in this study. These results suggest that nutrient densities are smaller in larger seeds, and small seeds have a larger "packaging cost" and thus are more protected than large seeds. The strong negative correlation between kernel weight and nutrient density, especially under stress (Figure 5), is a consequence of more N being concentrated per unit of starch in the kernel due to a reduction in synthesis and storage of carbohydrates (Peterson and Rendig, 2001; Ozturk and Aydin, 2004). In a diverse set of oat genotypes, Peterson et al. (2005) reported negative correlations ($P < 0.05$) between protein and GY (−0.59), and between oil and each of TKWT (−0.38) and percent groat (−0.42).

The biplot of PC analysis (Figure 5) proved to be a useful tool to visualize how traits in leaves, kernels and groats responded to stress treatments. Most traits had robust models with a large percentage of total variance accounted for by the first and second PCs. The stress treatments generally had comparable loadings on both PCs, and for the most part, traits under study responded

in a similar manner to the different stress treatments, including abiotic stress (i.e., temporal variation). This conclusion is confirmed by the variance components (Table 2) which were mostly accounted for by temporal variation and its interaction with stress treatments.

CONCLUSIONS

We quantified the complex interactions of midday differential canopy temperature (dT), C:N ratios, and nutrient densities in leaves, kernels and groats of oat crops subjected to biotic stresses caused by aphid feeding or by aphid-vectored virus and their combined effect on its grain yield, yield components, and grain composition during two years of contrasting rainfall and temperature regimes. Simple measurements at the boot stage of plant architecture (i.e., leaf area per plant, leaf area index, number of leaves and number of tillers per plant) and midday differential canopy temperature (dT) were indicative of how plants reacted to biotic stresses. Plant architectural differences caused by these stresses impacted dT, which in turn, negatively impacted grain yield and its components. Differences in nutrient densities caused by biotic stress impacted C:N ratios, which in turn influenced grain yield and its components. Stressed plants capable of maintaining larger C:N ratios in groats produced larger grain yields and larger number of kernels m^{-1}. These indirect relationships among plant architecture components, nutrient densities, dT, and C:N ratios, illustrate the complex interactions of biotic and abiotic stresses and their impact on grain yield and its components in oat.

ACKNOWLEDGMENTS

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